

Checklist of the continental fishes of the state of Chiapas, Mexico, and their distribution

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Abstract

An updated checklist of the distribution of fishes that inhabit the continental waters of the Mexican state of Chiapas is presented. The state was compartmentalized into 12 hydrological regions for the purpose of understanding the distribution of fish fauna across a state with large physiographic variance. The ichthyofauna of Chiapas is represented by 311 species distributed in two classes, 26 orders, 73 families, and 182 genera, including 12 exotic species. The families with the highest number of species were Cichlidae, Poeciliidae, Sciaenidae, Carangidae, Ariidae, Gobiidae, and Haemulidae. This study attempts to close gaps in knowledge of the distribution of ichthyofauna in the diverse hydrological regions of Chiapas, Mexico.

Keywords

Distribution, endemism, fish diversity, ichthyology, southern Mexico

Introduction

The hydrological wealth of Chiapas is manifested through its 72 perennial rivers and abundant streams, lakes, and ponds. The presence of large hydroelectric dams has significantly increased the surface area of the state's bodies of water (Velasco-Colín 1976). Chiapas has a coastline of 270 km and more than 70,000 hectares of estuaries and coastal lagoons (Contreras-Espinosa 2010), which favors the presence of rich fish diversity (Velasco-Colín 1976, Lozano-Vilano and Contreras-Balderas 1987, Rodiles-Hernández et al. 2005). Much of the state is located in the Usumacinta ichthyographic province/area of endemism (Miller et al. 2005, Matamoros et al. 2015), which means that its continental waters host a high number of endemic species, making Chiapas a freshwater biodiversity hotspot (Hudson et al. 2005, Matamoros et al. 2015).

Several attempts have been made to record continental water fish diversity in Chiapas through numerous works such as checklists, annotated checklists, books and scattered records in the literature (e.g. Velasco-Colín 1976, Lozano-Vilano and Contreras-Balderas 1987, Lazcano-Barrero and Vogt 1992, Tapia-García et al. 1998, Rodiles-Hernández et al. 1999, Rodiles-Hernández 2005, Rodiles-Hernández et al. 2005, 2013, Lozano-Vilano et al. 2007, González-Díaz et al. 2008, Espinosa-Pérez et al. 2011, Velázquez-Velázquez et al. 2013, Gómez-González et al. 2012, 2015). The first comprehensive publication on continental fishes of Chiapas was made by Velasco-Colín (1976), who reported 74 species distributed across 28 families. He also included brief information about the ecology, biology and distribution of several species and, in some cases, added relevant fishing information.

Subsequently Lozano-Vilano and Contreras-Balderas (1987) published an annotated checklist in which they registered 135 species belonging to 38 families in the state's continental waters. In addition to an increase in the number of data records, for the first time the distribution of fishes was associated with seven of the state's physiographic regions. Eighteen years later Rodiles-Hernández (2005) and Rodiles-Hernández et al. (2005) recorded 205 species in 44 families and 207 species in 45 families respectively. In the first study, distributions were reported at the level of the two main Chiapas river basins, the Grijalva-Usumacinta and the Coast of Chiapas, whereas, in the second study, the distributional geographic units were the Atlantic and the Pacific slope. Velázquez-Velázquez et al. (2013) was the last published attempt to summarize continental fishes of Chiapas. They reported 262 species across 57 families, and once again the geographic distribution units were the Grijalva and the Usumacinta River basins and the coast of Chiapas.

Two interesting trends emerge about the continental fishes of Chiapas. First, the number of recorded species has continued to increase over time likely due to an increase in sampling localities, implementation of new sampling techniques, new records and species descriptions. The second trend is related to the geographic units in which the state has been divided. For instance, Lozano-Vilano and Contreras-Balderas (1987) divided the state into seven physiographic regions, based on terrestrial relief. Most studies used broad delineations limited to the three major hydrologic regions (coast of Chiapas

and the Grijalva and Usumacinta River basins) masking detailed information on finer distributional patterns like localized endemism and drainage interconnections.

Therefore, the aim of this study is to provide an updated checklist of the continental fishes of Chiapas, including distribution data, based on extensive literature research and complemented with material deposited in the ichthyological collection of the Museum of Zoology at the University of Arts and Sciences of Chiapas (MZ-P-UNICACH). For the first time, we use finer scale geographic divisions for the state, implemented at the sub-basin level, following the National Institute of Statistics and Geography (INEGI 2010).

Materials and methods

The bulk of records came from the material of 204 species deposited in the ichthyological collection of the MZ-P-UNICACH Museum of Zoology (MZ-P-UNICACH, SEMARNAT: CHIS-PEC-210-03-09). In addition, we performed an extensive literature review for records of continental fishes of Chiapas. The checklists previously published by Lozano-Vilano and Contreras-Balderas (1987), Rodiles-Hernández (2005), Rodiles-Hernández et al. (2005), Espinosa-Pérez et al. (2011), and Velázquez-Velázquez et al. (2013) were taken as the basis for this work and were supplemented with publications by Lazcano-Barrero and Vogt (1992), Tapia-García et al. (1998), Rodiles-Hernández et al. (1999), Lozano-Vilano et al. (2007) and Gómez-González et al. (2012, 2015) who developed lists for particular regions of the state. We also included Castro-Aguirre et al. (1999) and Miller et al. (2005).

Species were systematically arranged by order and family following Nelson (2006). Genera and species were arranged alphabetically; scientific names and authorities were corroborated following Eschmeyer et al. (2016). Tolerance to salinity was based on Myers (1938).

The 12 geographical units for Chiapas (Figure 1) were utilized to determine the distribution of each species across the state. These 12 units were based on existing hydrological sub-basins of the state (INEGI 2010). The main rivers, ponds, lakes and coastal lagoons of each sub-basin are listed in Table 1.

Results

The continental fishes of the state of Chiapas are represented by two classes, 26 orders, 73 families, 182 genera and 311 species (Table 2), including 12 exotic species (*Ctenopharyngodon idella*, *Cyprinus carpio*, *Micropterus salmoides*, *Oncorhynchus mykiss*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Parachromis managuensis*, *Pterygoplichthys disjunctivus*, *Pterygoplichthys multiradiatus*, *Pterygoplichthys pardalis*, and *Tilapia zilli*). Only five species were endemic: the catfish *Lacantunia enigmatica*, the cichlids *Rocio ocotal* and *Thorichthys socolofi*, the killifish *Tlaloc hildebrandi* and the molly *Poecilia*

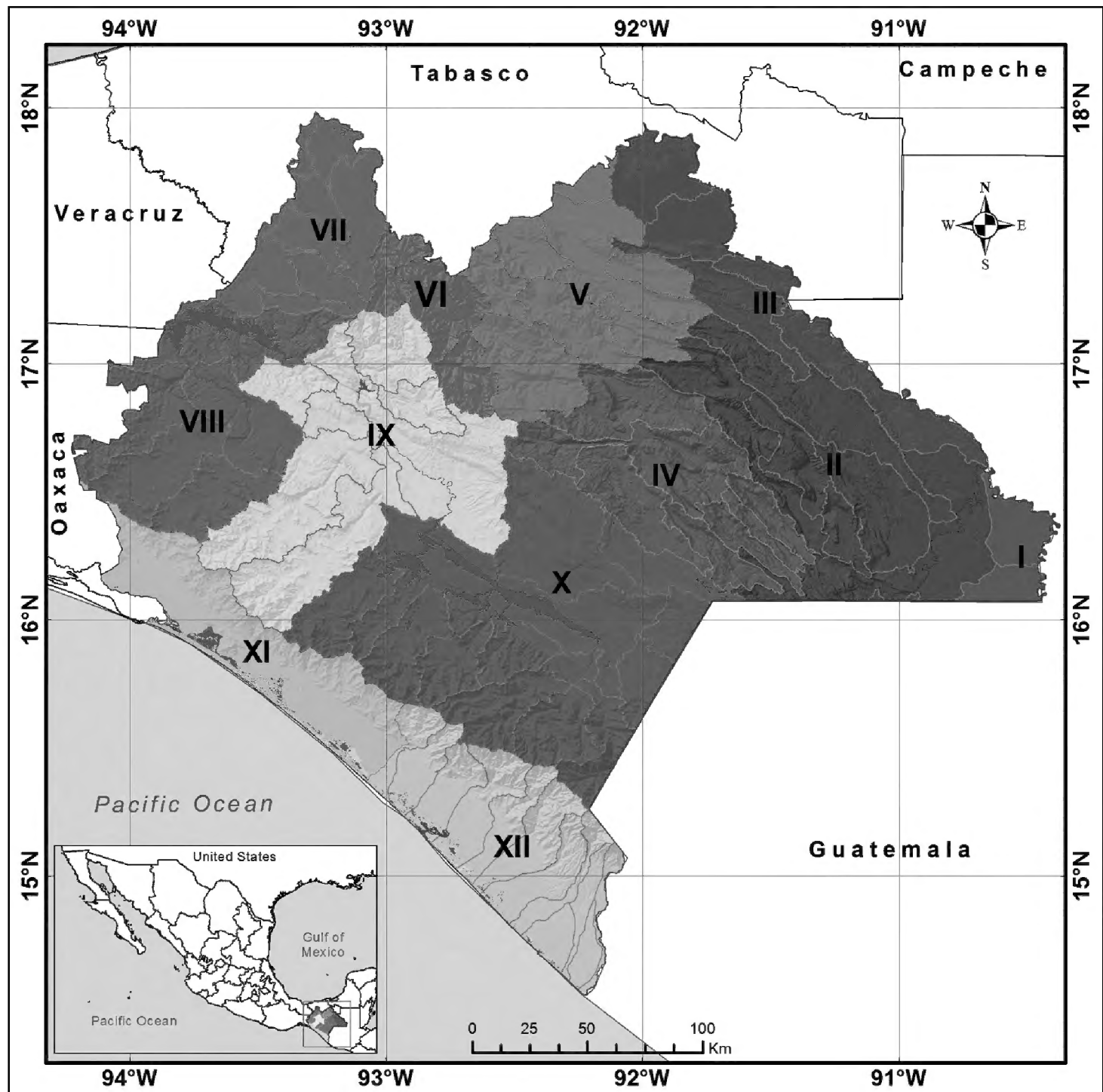


Figure 1. Geographical units for the study of the distribution of the fish fauna of the state of Chiapas: **I** (Usumacinta-Chixoy) **II** (Usumacinta-Lacantún) **III** (Usumacinta-Catazajá) **IV** (Usumacinta-Jataté) **V** (Grijalva-Tulijá) **VI** (Grijalva-Teapa) **VII** (Grijalva-Peñitas) **VIII** (Grijalva-Malpaso), **IX** (Grijalva-Chicoasén) **X** (Grijalva-La Angostura) **XI** (Costa-Itismo) **XII** (Costa-Soconusco).

thermalis. Based on species richness the most important families were: Cichlidae (35), Poeciliidae (29), Sciaenidae (18), Carangidae (17), Ariidae (16), Gobiidae (12), and Haemulidae (11). Almost all of these families, except the first two, contains peripheral species. These eight families represented 44.37% (138) of the state's total species richness. Thirteen species are included in risk categories under Mexican law (NOM-059-SEMARNAT-2010; SEMARNAT, 2010): *Poecilia sulphuraria* and *Tlaloc hildebrandi* are listed as endangered; *Priapella compressa*, *Thorichthys socolofi*, *Vieja hartwegi* and *Xiphophorus clemenciae* are listed as threatened; finally *Chiapaheros grammodes*, *Gambusia eurystoma*, *Hippocampus ingens*, *Potamarius nelsoni*, *Priapella intermedia*, *Rhamdia guatemalensis* and *Chuco intermedium* are listed as species under special protection. Based on general salinity

Table 1. Geographic units utilized to study the distribution of the fish fauna of Chiapas and sub-basins that form them.

Hidrological region	Basin	Sub-basin	Geographic unit
COSTA DE CHIAPAS	R. SUCHIATE AND OTHERS	R. Suchiate	Costa-Soconusco
		R. Cozoloapan	
		R. Cahuacán	
		Puerto Madero	
		R. Coatán	
		R. Huehuetán	
	R. HUIXTLA AND OTHERS	R. Huixtla	
		R. Despoblado	
		L. del Viejo y Tembladeras	
		R. Cacaluta	
		R. Sesecapa	
		R. Novillero	
	R. PIJJIAPAN AND OTHERS	R. Margaritas y Coapa	Costa-Istmo
		R. Pijijiapan	
		R. San Diego	
		El Porvenir	
		R. Jesús	
		L. de la Joya	
	MAR MUERTO	R. Zanatenco	
		Mar Muerto	
		R. La Punta	
		R. Las Arenas	
		R. Tapanatepec	
GRIJALVA - USUMACINTA	R. USUMACINTA	R. Usumacinta	Usumacinta-Catazajá
		R. Chacamax	
		R. Chacaljá	
	R. CHIXOY	R. Chixoy	Usumacinta-Chixoy
		R. Negro	
	R. GRIJALVA - VILLAHERMOSA	R. Viejo Mezcalapa	Grijalva-Peñitas
		R. Mezcalapa	
		R. Tzimbac	
		R. Zayula	
		R. Platanar	
		R. Paredón	
		R. Pichucalco	
		R. Tacotalpa	
		R. Samaria	
		R. de la Sierra	Grijalva-Teapa
		R. Almendro	
		R. Plátanos	
		R. Chacté	Grijalva.Tulijá
		R. Puxcatán	
		R. Macuspana	

Hidrological region	Basin	Sub-basin	Geographic unit
GRIJALVA - USUMACINTA		R. Shumulá	
		R. Yashijá	
		R. Tulijá	
		R. Bascá	
		R. Chilapa	
	R. GRIJALVA - TUXTLA GUTIÉRREZ	P. Nezahualcóyotl	Grijalva-Malpaso
		R. La Venta	
		R. Encajonado	
		R. Cintalapa	
		R. de Zoyatenco	
		R. Alto Grijalva	Grijalva-Chicoasén
		R. Hondo	
		R. Chicoasén	
		R. Suchiapa	
		Tuxtla Gutiérrez	
		El Chapopote	
		R. Santo Domingo	
	R. GRIJALVA - LA CONCORDIA	P. La Angostura	Grijalva-La Angostura
		R. Selegua	
		R. Lagartero	
		R. Aguacatenco	
		R. San Pedro	
		R. La Concordia	
		R. Grande o Salinas	
		R. Aguazurco	
		R. San Miguel	
		R. Yahuayita	
		R. Zacualpa	
		R. Tapizaca	
		R. Comitán	
	R. LACANTÚN	R. Lacantún	Usumacinta- Lacantún
		R. Ixcán	
		R. Chajul	
		R. Lacanjá	
		R. San Pedro	
		L. Miramar	
		R. Perlas	
		R. Jataté	Usumacinta-Jataté
		R. Azul	
		R. Tzaconejá	
		R. Margaritas	
		R. Santo Domingo	
		R. Seco	
		R. Caliente	
		R. Euseba	

Table 2. Systematic list of the continental waters ichthyofauna of Chiapas. Ecological classification: PF (Primary Freshwater), SF (Secondary Freshwater), PF (Peripheral Vicarious), PC (Peripheral Catadromous), P (Peripheral), Ex (Exotic).

No	Taxon	Ecological classification	Grijalva- La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Peñitas	Grijalva- Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta- Chixoy	Usumacinta-Catazajá	Costa-Istmo	Costa-Soconusco
Order Charcharhiniformes														
I Family Carcharhinidae														
1	<i>Carcharhinus leucas</i> (Müller & Henle, 1839)	P											x	
2	<i>Carcharhinus limbatus</i> (Müller & Henle, 1839)	P											x	x
3	<i>Carcharhinus cerdale</i> Gilbert, 1898	P											x	
4	<i>Rhizoprionodon longurio</i> (Jordan & Gilbert, 1882)	P											x	
5	<i>Negaprion brevirostris</i> (Poey, 1868)	P											x	
II Family Sphyrnidae														
6	<i>Sphyrna tiburo</i> (Linnaeus, 1758)	P											x	
Order Pristiformes														
III Family Pristidae														
7	<i>Pristis pectinata</i> Latham, 1794	P											x	
8	<i>Pristis microdon</i> Latham, 1794	P											x	
Order Rhinobatiformes														
IV Family Rhinobatidae														
9	<i>Pseudobatos glaucostigma</i> (Jordan & Gilbert, 1883)	P											x	
Order Myliobatiformes														
V Family Urotrygonidae														
10	<i>Urotrygon aspidura</i> (Jordan & Gilbert, 1882)	P											x	
11	<i>Urotrygon chilensis</i> (Günther, 1872)	P											x	
12	<i>Urotrygon munda</i> Gill, 1863	P											x	
13	<i>Urotrygon nana</i> Miyake & McEachran, 1998	P											x	
14	<i>Urotrygon rogersi</i> (Jordan & Starks, 1895)	P											x	
VI Family Dasyatidae														
15	<i>Hypanus longus</i> (Garman, 1880)	P											x	x
16	<i>Himantura pacifica</i> (Beebe & Tee-Van, 1941)	P											x	x
VII Family Myliobatidae														
17	<i>Aetobatus laticeps</i> Gill, 1865	P											x	x
VIII Family Rhinopteridae														
18	<i>Rhinoptera steindachneri</i> Evermann & Jenkins, 1891	P											x	x
Order Lepisosteiformes														
IX Family Lepisosteidae														
19	<i>Atractosteus tropicus</i> Gill, 1863	PF				x				x	x	x	x	x
Order Elopiformes														
X Family Elopidae														
20	<i>Elops affinis</i> Regan, 1909	P											x	x
XI Family Megalopidae														
21	<i>Megalops atlanticus</i> Valenciennes, 1847	P				x						x		

No	Taxon	Ecological classification	Grijalva- La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Peñitas	Grijalva- Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta- Chixoy	Usumacinta-Catazajá	Costa-Istmo	Costa-Soconusco
Order Albuliformes														
XII Family Albulidae														
22	<i>Albula esuncula</i> (Garman, 1899)	P											x	
Order Anguiliformes														
XIII Family Ophichthidae														
23	<i>Myrichthys xysturus</i> (Jordan & Gilbert, 1882)	P											x	
24	<i>Ophichthus zophochir</i> Jordan & Gilbert, 1882	P											x	x
Order Clupeiformes														
XIV Family Pristigasteridae														
25	<i>Pliosteostoma lutipinnis</i> (Jordan & Gilbert, 1882)	P											x	
26	<i>Odontognathus panamensis</i> (Steindachner, 1876)	P											x	
27	<i>Opisthopterus dovii</i> (Günther, 1868)	P												x
XV Family Engraulidae														
28	<i>Anchoa argentivittata</i> (Regan, 1904)	P											x	
29	<i>Anchoa curta</i> (Jordan & Gilbert, 1882)	P											x	x
30	<i>Anchoa ischana</i> (Jordan & Gilbert, 1882)	P											x	x
31	<i>Anchoa lucida</i> (Jordan & Gilbert, 1882)	P											x	x
32	<i>Anchoa mitchilli</i> (Valenciennes, 1848)	P										x		
33	<i>Anchoa mundeola</i> (Gilbert & Pierson, 1898)	P											x	x
34	<i>Anchoa walkeri</i> Baldwin & Chang, 1970	P											x	
35	<i>Anchoa starksii</i> (Gilbert & Pierson, 1898)	P											x	x
36	<i>Anchovia macrolepidota</i> (Kner, 1863)	P											x	x
XVI Family Clupeidae														
37	<i>Dorosoma anale</i> Meek, 1904	P (V)	x	x	x	x	x	x		x	x	x		
38	<i>Dorosoma petenense</i> (Günther, 1867)	P (V)	x	x	x	x	x	x		x	x	x		
39	<i>Harengula thrissina</i> (Jordan & Gilbert, 1882)	P											x	
40	<i>Lile gracilis</i> Castro-Aguirre & Vivero, 1990	P											x	x
41	<i>Lile nigrofasciata</i> Castro-Aguirre, Ruiz-Campos & Balart, 2005	P											x	x
42	<i>Opisthonema libertate</i> (Günther, 1867)	P											x	x
43	<i>Opisthonema medirastre</i> Berry & Barret, 1964	P											x	
Order Gonorynchiformes														
XVII Family Chanidae														
44	<i>Chanos chanos</i> (Forsskal, 1775)	P											x	x
Order Cypriniformes														
XVIII Family Cyprinidae														
45	<i>Ctenopharyngodon idella</i> (Valenciennes, 1844) ^{Ex}	Ex				x	x	x		x	x	x		
46	<i>Cyprinus carpio</i> (Linnaeus, 1758) ^{Ex}	Ex	x	x				x				x		
XIX Family Catastomidae														
47	<i>Ictiobus meridionalis</i> (Günther, 1868)	PF			x	x	x	x		x	x	x		
Order Characiformes														
XX Family Characidae														
48	<i>Astyanax aeneus</i> (Günther, 1860)	PF	x	x	x	x	x	x	x	x	x	x	x	x
49	<i>Bramocharax</i> sp.	PF						x		x	x	x		

[illegible]

[illegible]

[illegible]

[illegible]

No	Taxon	Ecological classification	Grijalva- La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Peñitas	Grijalva- Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta- Chixoy	Usumacinta-Catazajá	Costa-Istmo	Costa-Soconusco
215	<i>Menticirrhus panamensis</i> (Steindachner, 1876)	P											x	
216	<i>Micropogonias altipinnis</i> (Günther, 1864)	P											x	x
217	<i>Micropogonias megalops</i> (Gilbert, 1890)	P											x	
218	<i>Nebris occidentalis</i> Vaillant, 1897	P												x
219	<i>Paralonchurus goodei</i> Gilbert, 1898	P												x
220	<i>Stellifer</i> cf. <i>walkeri</i>	P												x
LII Family Mullidae														
221	<i>Pseudupeneus grandisquamis</i> (Gill, 1863)	P											x	
LIII Family Kyphosidae														
222	<i>Kyphosus elegans</i> (Peters, 1869)	P											x	x
LIV Family Chaetodontidae														
223	<i>Chaetodon humeralis</i> Günther, 1860	P											x	x
LV Family Cichlidae														
224	<i>Amphilophus trimaculatus</i> (Günther, 1867)	SF		x	x								x	x
225	<i>Astatheros macracanthus</i> (Günther, 1864)	SF	x		x								x	x
226	<i>Chiapaheros grammodes</i> (Taylor & Miller, 1980)	SF	x	x										
227	<i>Cincolichthys pearsei</i> (Hubbs, 1936)	SF		x	x	x		x		x	x	x		
228	<i>Chuco intermedium</i> (Günther, 1862)	SF	x				x	x	x	x	x	x		
229	<i>Cribroheros robertsoni</i> (Regan, 1905)	SF				x						x		
230	<i>Kihnichthys ufermanni</i> Allgayer, 2002	SF								x	x	x		
231	<i>Maskaheros argenteus</i> (Allgayer, 1991)	SF				x				x	x	x		
232	<i>Maskaheros regani</i> (Miller, 1974)	SF		x	x									
233	<i>Mayaheros urophthalmus</i> (Günther, 1862)	SF			x	x				x	x	x		
234	<i>Oreochromis aureus</i> (Steindachner, 1864) ^{Ex}	Ex								x				
235	<i>Oreochromis mossambicus</i> (Peters, 1852) ^{Ex}	Ex	x		x					x				
236	<i>Oreochromis niloticus</i> (Linnaeus, 1758) ^{Ex}	Ex	x	x	x	x	x	x		x	x	x	x	x
237	<i>Oscura heterospila</i> (Hubbs, 1936)	SF				x		x				x		
238	<i>Parachromis friedrichsthalii</i> (Heckel, 1840)	SF								x	x	x		
239	<i>Parachromis managuensis</i> (Günther, 1867) ^{Ex}	Ex		x	x	x		x		x	x	x		x
240	<i>Paraneetroplus gibbiceps</i> (Steindachner, 1864)	SF					x	x						
241	<i>Petenia splendida</i> Günther, 1862	SF		x	x	x		x		x	x	x		
242	<i>Rocio ocotal</i> Schmitter-Soto, 2007	SF								x				
243	<i>Rocio octofasciata</i> (Regan, 1903)	SF				x		x		x	x	x		
244	<i>Theraps irregularis</i> Günther, 1862	SF							x	x	x	x		
245	<i>Thorichthys meeki</i> Brind, 1918	SF				x				x	x	x		
246	<i>Thorichthys pasionis</i> (Rivas, 1962)	SF				x					x	x		
247	<i>Thorichthys socolofi</i> (Miller & Taylor, 1984)	SF						x		x				
248	<i>Thorichthys helleri</i> (Steindachner, 1864)	SF			x	x	x	x	x	x	x	x		
249	<i>Trichromis salvini</i> (Günther, 1862)	SF			x	x		x	x	x	x	X		
250	<i>Tilapia zilli</i> (Gervais, 1848) ^{Ex}	Ex	x	x	x									
251	<i>Rheoheros coeruleus</i> (Stawikowski & Werner, 1987)	SF						x						
252	<i>Rheoheros lentiginosus</i> (Steindachner, 1864)	SF					x	x	x	x	x	x		
253	<i>Vieja bifasciata</i> (Steindachner, 1864)	SF				x	x	x		x	x	x		

No	Taxon	Ecological classification	Grijalva- La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Peñitas	Grijalva- Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta- Chixoy	Usumacinta-Catazajá	Costa-Istmo	Costa-Soconusco
LXIV Family Acanthuridae														
289	<i>Acanthurus xanthopterus</i> Valenciennes, 1835	P											x	
LXV Family Sphyraenidae														
290	<i>Sphyraena ensis</i>	P											x	
LXVI Family Trichiuridae														
291	<i>Trichiurus nitens</i> Garman, 1899	P												x
LXVII Family Scombridae														
292	<i>Scomberomorus sierra</i> Jordan & Starks, 1895	P											x	x
Order Pleuronectiformes														
LXVIII Family Paralichthyidae														
293	<i>Citharichthys gilberti</i> Jenkins & Evermann, 1889	P											x	x
294	<i>Cyclopsetta panamensis</i> (Steindachner, 1876)	P											x	
295	<i>Etropus crossotus</i> Jordan & Gilbert, 1882	P											x	
296	<i>Syacium latrifrons</i> (Jordan & Gilbert, 1882)	P											x	
297	<i>Syacium ovale</i> (Günther, 1864)	P											x	
LXIX Family Achiridae														
298	<i>Achirus mazatlanus</i> (Steindachner, 1869)	P											x	x
299	<i>Achirus scutum</i> (Günther, 1862)	P											x	x
300	<i>Achirus zebrinus</i> Clark, 1936	P											x	
301	<i>Trinectes fimbriatus</i> (Günther, 1862)	P												x
302	<i>Trinectes fonsecensis</i> (Günther, 1862)	P											x	x
LXX Family Cynoglossidae														
303	<i>Symphurus chabanaudi</i> Mahadeva & Munroe, 1990	P												x
304	<i>Symphurus elongatus</i> (Günther, 1868)	P											x	
305	<i>Symphurus melanurus</i> Clark, 1936	P											x	
Order Tetraodontiformes														
LXXI Family Balistidae														
306	<i>Pseudobalistes naufragium</i> (Jordan & Starks, 1895)	P											x	x
LXXII Family Tetraodontidae														
307	<i>Arothron meleagris</i> (Bloch & Schneider, 1801)	P												x
308	<i>Sphoeroides annulatus</i> (Jenyns, 1842)	P											x	x
309	<i>Sphoeroides rosenblatti</i> Bussing, 1996	P											x	x
LXXIII Family Diodontidae														
310	<i>Diodon holocanthus</i> Linnaeus, 1758	P												x
311	<i>Diodon hystrix</i> Linnaeus, 1758	P											x	x
Total species by geographical units			23	31	45	55	36	46	11	63	54	72	174	153

tolerance, and excluding exotic species, 16 are primary freshwater fishes, 65 secondary freshwater fishes, and the rest of the species are peripheral (Table 2).

Of the 12 geographical units (Fig. 1), the region with the highest number of species was Costa-Istmo with 174 species, followed by Costa-Soconusco with 153 species and

the third was Usumacinta-Catazajá with 72 species. The region with the lowest recorded species was Usumacinta-Jataté with only 11 species. Numbers of species from other geographical units are presented in Table 2. Spatially, *Astyanax aeneus* and *Rhamdia guatemalensis* appeared in all regions within Chiapas. Other species with widespread distributions were *Poecilia sphenops* and the exotic cichlid *Oreochromis niloticus* (10 and 11 regions respectively). *Atherinella alvarezi*, *Brycon guatemalensis*, *Dorosoma anale*, *Dorosoma petenense*, and *Ictalurus meridionalis* were distributed in nine regions, while *Aplodinotus grunniens*, *Gambusia sexradiata*, *Ophisternon aenigmaticum*, *Parachromis managuensis*, *Poecilia mexicana*, *Pseudoxiphophorus bimaculatus*, and *Thorichthys helleri* were recorded in eight regions.

Eight marine species were newly recorded as species found in continental waters of Chiapas: *Acanthurus xanthopterus*, *Atherinella panamensis*, *Fistularia commersonii*, *Halichoeres dispilus*, *Nicholsina denticulata*, *Orthopristis chalceus*, *Stegastes flavilatus*, and *Sphyrna ensis*.

Discussion

Knowledge of the species richness of continental fishes in Chiapas has increased significantly over recent years compared to previous assessments (e.g. Rodiles-Hernández et al. 2005, Velázquez-Velázquez et al. 2013). The increasing number of known species is the result of collections in new localities, improvement in sampling effort, and larger systematic and taxonomic reviews. For instance, an extensive literature search provided many reports of marine species, principally elasmobranchs, in continental waters of Chiapas by Castro-Aguirre et al. (1999). The large increment in the checklist is due to the inclusion of many elasmobranchs fishes that were included previously in the work of Castro-Aguirre et al. (1999), but that for some reason these records were ignored in more recent accounts of fishes in the continental waters of Chiapas. Castro-Aguirre et al. (1999) reported 41 species of marine fishes including an important number of sharks and sting-rays in the state continental water.

Two species previously reported were removed from the list of species in Chiapas in this study: the American eel (*Anguilla rostrata*) and the Mexican tetra (*Astyanax mexicanus*). The American eel was mentioned in the pioneering work of Velasco-Colín (1976), and since then listed in subsequent publications (Lozano-Vilano and Contreras-Balderas 1987, Rodiles-Hernández 2005, Rodiles-Hernández et al. 2005, Espinosa-Pérez et al. 2011, Velázquez-Velázquez et al. 2013). However, these works do not offer precise geographical locations for these species and there are no vouchered specimens from Chiapas in national or international collections. Records of the Mexican tetra in Chiapas probably contain misidentifications as mentioned by Lozano-Vilano and Contreras-Balderas (1987) and Ornelas-García et al. (2008), thus supporting the absence of this species in Southern Mexico. We have included Important and recent taxonomic changes made in the family Cichlidae by McMahan et al. (2015) and Říčan et al. (2016), the family Poeciliidae by Palacios et al. (2016) and the family Profundulidae by Morcillo et al. (2016).

More than 1000 species of fishes have been reported in the continental waters of Mexico, including freshwater and estuarine fishes (Espinosa-Pérez 2014). The continental fish fauna of the state of Chiapas represents approximately 29% of the continental fish fauna of the entire country of Mexico. This highlights the great diversity of fishes inhabiting continental environments of Chiapas as a result of the region's hydrological wealth. Our results are comparable with those from other southern Mexican states such as Quintana Roo (Schmitter-Soto 1998), Oaxaca (Martínez-Ramírez et al. 2004) and Tabasco (Espinosa-Pérez and Daza-Zepeda 2005).

The native obligate freshwater (primary and secondary) species of Chiapas accounted for only 26% (81) of the state's total species richness. The communities are dominated by peripheral species, many of them permanent (vicarious) residents of the Grijalva-Usumacinta basin (e.g. *Aplodinotus grunniens*, *Eugerres mexicanus*, *Hyporhamphus mexicanus*, *Strongylura hubbsi*), but the majority are distributed in brackish environments of the Costa-Itzmo and Costa-Soconusco sub-basins. Some of these communities also permeate nearby rivers. In terms of slopes, the Pacific slope houses 68% of the state fish fauna while the Gulf slope houses 33%, and in terms of regional diversity the Usumacinta region is considered one of the most diverse areas of endemism for freshwater fishes in Central America; however, from a biogeographical perspective the entire Central American region has a depauperate freshwater fish fauna compared with the vast diversity of ostariophysan fishes found in North and South America (Miller 1966, Myers 1966, Bussing 1985, Chakrabarty and Albert 2011, Matamoros et al. 2015). This could explain the presence of a great number of peripheral species recorded in the continental environments of Chiapas. This pattern is comparable with other countries of Central America such as Guatemala (Kihn-Pineda et al., 2006), Honduras (Matamoros et al. 2009) and El Salvador (McMahan et al. 2013).

Mexican law protects thirteen freshwater species; however, *Rhamdia guatemalensis* is quite abundant in Chiapas and possesses a wide distribution through other geographic areas of Mexico and Central America (Miller et al. 2005, Hernández et al. 2015). Its inclusion should be reconsidered in the NOM-059-SEMARNAT-2010. Conversely, we suggest that Mexican laws should consider including *Lacantunia enigmatica*, *Rhamdia laluchensis* and *Vieja breidohri* as protected species on the grounds of their restricted distribution.

Since the pioneering work of Lozano-Vilano and Contreras-Balderas (1987), this is the first time the state of Chiapas has been regionalized in a more detailed scale than the three great basins (Grijalva, Usumacinta and Costa). Lozano-Vilano and Contreras-Balderas (1987) proposed seven physiographic regions; however, their proposal was based on physiographic characteristics of landscape relief rather than hydrology. In this study we present a zonation based on the level of hydrological regions (sub-basins), which provides a more robust delineation of the geographical areas for fish species and facilitates a closer examination of the distribution of endemic species. This approach demonstrates that gaps in knowledge of the distribution of species is still quite large and indicates that some portions of the territory remain moderately sampled or unex-

plored. For instance, the Usumacinta-Jataté sub-basin, with only 11 species recorded, remains largely unexplored. The detailed regionalization of Chiapas highlights the necessity of increasing sampling efforts in certain zones.

Although hydrological regions Grijalva, Usumacinta and Costa of Chiapas have been used in previous studies to discover endemism in the state (Rodiles-Hernández, 2005, Rodiles-Hernández et al. 2005, Velázquez-Velázquez et al. 2013), the zonation of our study allows identification of smaller geographic units, permitting us to be more specific in studies of endemism. Thus, the distribution of endemic species in Chiapas includes: *Lacantunia enigmatica* in Usumacinta-Lacantún, *Rocio ocotal* in Usumacinta-Lacantún, *Thorichthys socolofi* in Grijalva-Tulijá and Usumacinta-Lacantún, *Tlaloc hildebrandi* in Grijalva-Teapa and Usumacinta-Jataté, and *Poecilia thermalis* in Grijalva-Teapa. Of the 12 units, Usumacinta-Lacantún stands out as it houses three endemic species: *Lacantunia enigmatica*, *Rocio ocotal*, and *Thorichthys socolofi*.

Forty years of scientific research on the continental fish fauna of Chiapas has gone a long way since the work of Velasco-Colín (1976). However, this does not seem nearly enough time to completely finish to record the real extend of the state species richness with its distribution. In this work we present distributional data at 12 geographic units. However, although this is the finest distributional scale for the state, a major goal should be to complete distributional data for the 92 existing sub-drainages in the state. Many of these water bodies have never been sampled either for lack of financial resources or because they are located in remote areas of the state.

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